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ADVANCES IN CICHLID RESEARCH

Ancyrocephalidae (Monogenea) of Lake Tanganyika: IV: *Cichlidogyrus* parasitizing species of Bathybatini (Teleostei, Cichlidae): reduced host-specificity in the deepwater realm?

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Abstract Lake Tanganyika's biodiversity and endemicity sparked considerable scientific interest. Its monogeneans, minute parasitic flatworms, have received renewed attention. Their host-specificity and simple life cycle render them ideal for parasite speciation research. Because of the wide ecological and phylogenetic range of its cichlids, Lake Tanganyika is a "natural experiment" to contrast factors influencing monogenean speciation. Three representatives of Bathybatini (*Bathybates minor*, *B. fasciatus*, *B. vittatus*), endemic predatory non-littoral cichlids, host a single dactylogyridean monogenean species. It is new to science and described as *Cichlidogyrus casuarinus* sp. nov. This species and *C. nshomboi* and *C. centesimus*, from which it differs by the distal end of the accessory piece of the male apparatus and the length of its heel, are the only *Cichlidogyrus* species with spirally coiled thickening of the penis wall. In *Cichlidogyrus*, this feature was only found in parasites of endemic Tanganyika tribes. The seemingly species-poor *Cichlidogyrus* community of Bathybatini may be attributed to meagre host isolation in open water. The new species infects cichlids that substantially differ phylogenetically and ecologically. This may be an

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adaptation to low host availability. *Cichlidogyrus* species infecting African Great Lake cichlids are summarized and proposed as model for the influence of host ecology on disease transmission.

Keywords *Bathybates* · *Hemibates* · Perciformes · Platyhelminthes · Dactylogyridea · Host range

Introduction

Lake Tanganyika's biodiversity awed scientists from the very beginning of its exploration by Western science (e.g. Woodward, 1859 on gastropod diversity). Lake Tanganyika is only surpassed in depth and age by Lake Baikal and hosts a remarkable set of radiations of invertebrates and cichlid and non-cichlid fishes (Fryer, 1991). Its cichlid assemblage is behaviourally, genetically and morphologically the most diverse of all African Great Lakes. This differs from e.g. Lakes Malawi and Victoria, whose more speciose cichlid flocks almost entirely consist of mouthbrooding haplochromines (Snoeks, 2000). In other aquatic biodiversity hotspots, detailed parasite surveys of fishes revealed an impressive quantity of undiscovered species (e.g. coral reefs: Justine et al., 2010, 2012; Balkan freshwater: Vanhove et al., 2014). In Lake Tanganyika, parasitological work is relatively scarce and fragmentary. Indeed, while several aquatic parasite taxa are reported, such as Pentastomida (de Beauchamp, 1914; Hett, 1924; Fain, 1961), Isopoda, Copepoda (Fryer, 1968), Cestoda (de Beauchamp, 1914; Fuhrmann & Baer, 1925; Prudhoe, 1951), Digeneans, Acanthocephala (Prudhoe, 1951) and Hirudinea (Moore, 1938, Sciacchitano, 1962) (see Coulter, 1991 for an overview), few of them, let alone few host taxa, have been investigated in depth. The diversity of Lake Tanganyika fish parasites has recently gained renewed attention (Vanhove et al., 2011a, b; Gillardin et al., 2012; Muterezi Bukinga et al., 2012; Kilian & Avenant-Oldewage, 2013; Raeymaekers et al., 2013). Particularly interesting when studying assemblages of closely related and sympatrically occurring fishes are monogenean flatworms (Pariselle et al., 2003b). They have a simple (one host) life cycle and a relatively high host-specificity, often infecting one or a few closely related species. This ensures a close relationship with their host species. Conversely, a cichlid fauna like Lake Tanganyika's may set the ideal stage to contrast host factors that have been suggested to influence parasite communities, such as diet (Poulin, 1995; Choudhury & Dick, 2000; Hemmingsen et al., 2000; Luque & Poulin, 2008; Mwita & Nkwengulila, 2008), (social) behaviour including dispersal and shoaling (Sasal & Morand, 1998; Takemoto et al., 2005; Mwita & Nkwengulila, 2008), and environmental conditions (Machado et al., 1995; Luque & Poulin, 2008).

Worldwide, most monogenean species described from cichlid hosts belong to *Cichlidogyrus* Paperna, 1960 (see Pariselle & Euzet, 2009). This parasite genus is often classified under Ancyrocephalidae, though it should be noted that this flatworm family probably does not form a monophyletic group. Its representatives may have to be considered members of Dactylogyridae (Kritsky & Boeger, 1989; Šimková et al., 2003; Plaisance et al., 2005; Šimková et al., 2006). In Lake Tanganyika, *Cichlidogyrus* species were described from the endemic littoral cichlid tribes Ectodini (Vanhove et al., 2011b) and Tropheini (Gillardin et al., 2012), from the piscivorous Boulengerochromini and from Tanganyika representatives of the non-endemic genera *Astatotilapia* Pellegrin 1904a, *Oreochromis* Günther, 1889 and *Tylochromis* Regan, 1920 (see Muterezi Bukinga et al., 2012). It is suggested that the morphology of these monogeneans reflects to a certain extent the phylogenetic affinities of their hosts. Based on the morphology of their haptoral and genital hard parts, several of these *Cichlidogyrus* species are similar to their congeners infecting non-Tanganyika cichlids related to their Tanganyika hosts. This is the case for the parasites of the non-endemic Haplochromini, Tylochromini (sensu Poll, 1986) and Oreochromini (sensu Schwarzer et al., 2009) as well as for those infecting Tropheini, an endemic group which phylogenetically clusters under Haplochromini sensu lato (Salzburger et al., 2002, 2005). Other endemic Tanganyika cichlid lineages seem to host *Cichlidogyrus* species with features that are found nowhere else in the genus. This is the case for the haptoral configuration of some parasites of Ectodini and for the spirally-coiled wall of the copulatory tube (penis) in species infecting Ectodini and Boulengerochromini (Vanhove et al., 2011b; Muterezi Bukinga et al., 2012).

Bathybatini is an endemic Tanganyika tribe with an entirely different ecology than the ones hitherto

scrutinised for monogeneans. According to Poll (1986) it contains *Bathybates* Boulenger, 1898 and *Hemibates* Regan, 1920. Takahashi (2003), however, also included the members of Trematocarini sensu Poll (1986). Depending on the markers used, molecular data corroborate this affinity, or alternatively warrant the erection of three tribes to accommodate these species, namely Bathybatini, Hemibatini and Trematocarini (Koblmüller et al., 2005, 2008; Kirchberger et al., 2012). Bathybatines are maternal mouthbrooders; they are piscivores mostly inhabiting deep water. Given the little barriers to geneflow in this habitat (Kirchberger et al., 2012 and references therein), we hypothesize that little isolation takes place within their parasite community as well. We expect this leads to a species-poor *Cichlidogyrus* community. Indeed, within the littoral tribe Tropheini, stenotopic cichlids with highly structured populations have been suggested to host more *Cichlidogyrus* species than more eurytopic representatives that are better dispersers (Vanhove, 2012). Moreover, the *Cichlidogyrus* fauna of Tropheini displays a relatively high host-specificity. These parasite species are often confined to one, or some closely related tropheine host species. We explore whether this pattern found in the littoral zone also holds for the deepwater realm.

Materials and methods

Host fishes were purchased from fishermen or at fish markets and identified in situ by Donatien Muzumani Risasi (Centre de Recherche en Hydrobiologie-Uvira, D.R.Congo) or Stephan Koblmüller (Karl-Franzens University Graz, Austria) (for sampling details, see taxonomic account in the present paper, and see Van Steenberge et al., 2011). After dissection, fresh gills were inspected in situ for monogenean parasites using a stereomicroscope; some gills were fixed and preserved in absolute ethanol until further inspection in the lab. Monogeneans were isolated using a dissection needle and mounted on a slide under a coverslip in either glycerine ammonium picrate (Malmberg, 1957) or Hoyer's medium (see Humason, 1979).

Pictures and measurements of haptoral and genital hard parts were taken based on Gussev (1962) using a Leica DM2500 microscope at a magnification of 100x (oil immersion, 10× ocular) with LAS v.3.6 software and a DFC 425 Leica camera. The numbering of haptoral parts was adopted from ICOPA IV (Euzet & Prost, 1981); the terminology follows Pariselle & Euzet (1995a) (i.e. "uncinuli" for marginal hooks). The metrics taken are illustrated in Fig. 1. Measurements are in micrometers and presented as the average ± the standard deviation (when the number of measurements, *n*, is at least 30), with range and number of measured specimens in parentheses. Type material was deposited in the invertebrate collection of the Royal Museum for Central Africa (Tervuren, Belgium) (RMCA) and in the Muséum National d'Histoire Naturelle (Paris, France) (MNHN). Symbiotype and host vouchers (Frey et al., 1992; Brooks, 1993) were deposited in the RMCA. Host nomenclature follows Eschmeyer (2013).

Results

All specimens retrieved belong to a single hitherto undescribed species of *Cichlidogyrus* Paperna, 1960 (sensu Paperna, 1960; Pariselle et al., 2003a): Ancyrocephalidae (but see "Introduction" section). Three pairs of cephalic glands. Two posterior ocelli with crystalline lenses. Two small anterior ocelli (not always present or visible on mounted specimens). Median muscular pharynx. Simple intestinal caeca joined posteriorly. Two pairs of anchors, one dorsal and one ventral. Two transverse bars, one dorsal with two auricles, one ventral curved and articulated. Fourteen uncinuli. Median posterior testis. Vas deferens on right side, not encircling intestinal caecum. Seminal vesicle present. One prostatic reservoir. Male apparatus (MA) (also referred to as male copulatory organ, MCO) with penis and accessory piece (the latter not always present: Vanhove et al., 2011b), auxiliary plate sometimes present. Median pretesticular ovary. Sub-median vaginal opening. Sclerotised vagina sometimes visible. Seminal receptacle present. Gill parasites of African and Levantine Cichlidae, Cyprinodontidae and Nandidae. The proposed species new to science is described below.

Cichlidogyrus casuarinus sp. nov. Pariselle, Muterezi Bukinga and Vanhove (Figs. 2, 3; Table 1)

Type host: Bathybates minor Boulenger 1906b (symbiotype: MRAC B0-12-P-520 (host of holotype and paratype); host of additional paratypes: MRAC B0-12-P-524)

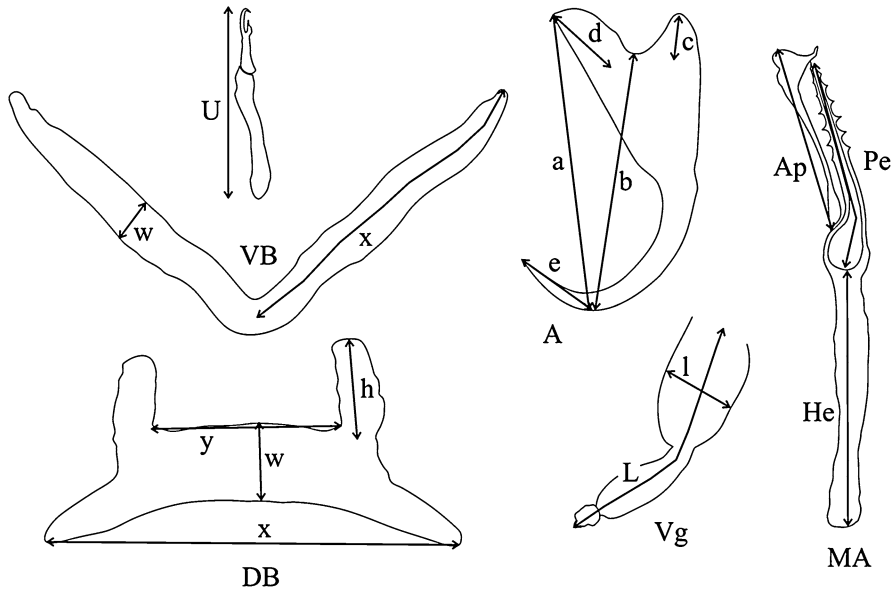


Fig. 1 Measurements used to study the new *Cichlidogyrus* species. (DB) Dorsal transverse bar: *h* length of dorsal bar auricle, *w* dorsal bar maximum width, *x* dorsal bar total length, *y* distance between auricles. (A) Anchor: *a* anchor total length, *b* anchor blade length, *c* anchor shaft length, *d* anchor guard length, *e* anchor point length. (MA) Male apparatus: *Ap* accessory piece length, *Pe* penis total length, *He* heel length. (U) Uncinuli length. (VB) Ventral transverse bar: *w* ventral bar maximum width, *x* length of one ventral bar branch. (Vg) Vagina: *L* vagina total length, *l* vagina width

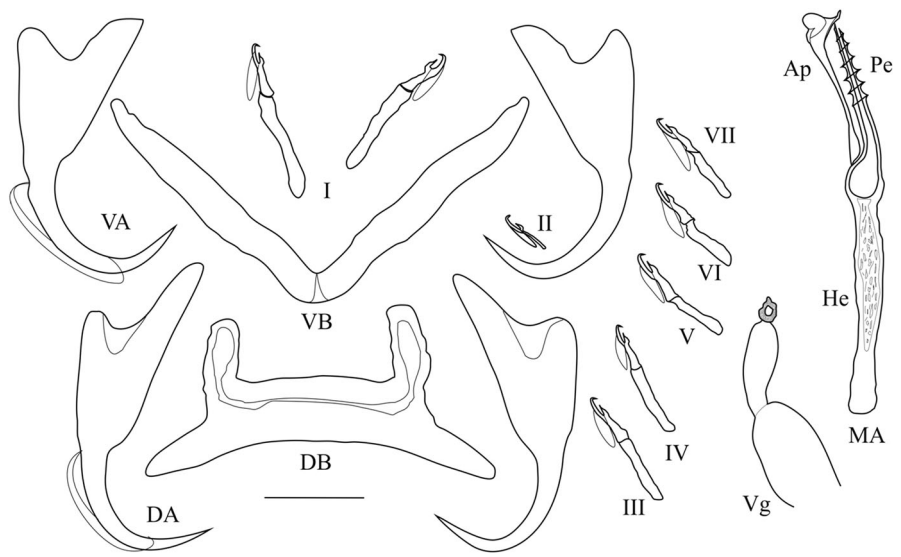


Fig. 2 Haptoral and genital hard parts of *Cichlidogyrus casuarinus* sp. nov. *Ap* accessory piece, *DB* dorsal transverse bar, *DA* dorsal anchor, *He* heel, *MA* male apparatus, *Pe* penis, *VB* ventral transverse bar, *VA* ventral anchor, *Vg* vagina, *I–VII* uncinuli. *Scale bar* 20 μm

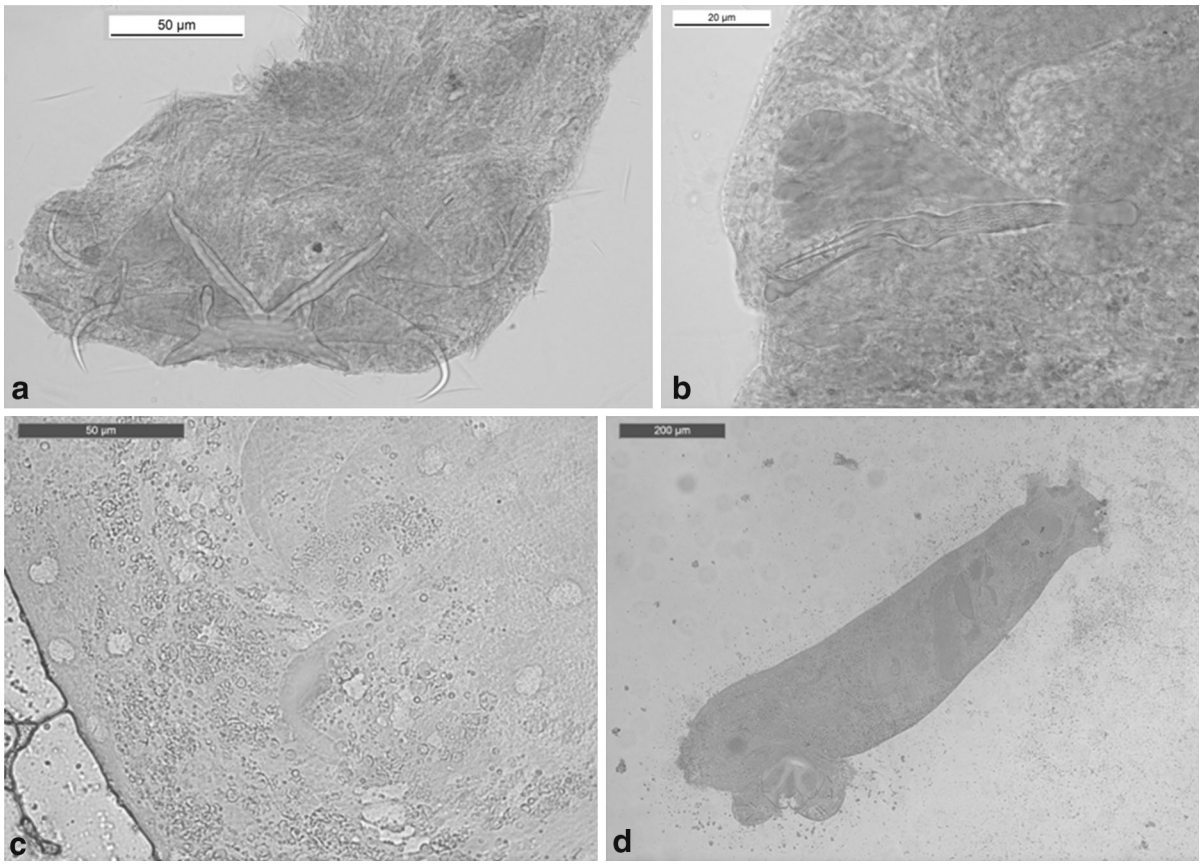


Fig. 3 Micrographs of *Cichlidogyrus casuarinus* sp. nov. fixed in glycerine ammonium picrate. **a** Haptor, **b** male copulatory organ, **c** vagina, **d** whole mount

Table 1 Overview of *Cichlidogyrus casuarinus* sp. nov. and *C.* cf. *casuarinus* sp. nov. findings reported

Parasite species	Host species	Locality	Date
Cichlidogyrus casuarinus sp. nov.	*Bathybates fasciatus* Boulenger, 1901	Kilomoni Market, Uvira, D.R.Congo	March 2013
	B. minor Boulenger 1906b (type host)	Mpala, D.R.Congo (type locality)	April 21st, 2010
		Kilomoni Market, Uvira, D.R.Congo	March 2013
	B. vittatus Boulenger, 1914	Mpala, D.R.Congo	April 21st, 2010
Cichlidogyrus cf. *casuarinus* sp. nov.	*B. fasciatus*	Kilomoni Market, Uvira, D.R.Congo	September 9th, 2013
		Kinindo Market, Bujumbura, Burundi	September 5th, 2013
	B. leo Poll, 1956	Kilomoni Market, Uvira, D.R.Congo	September 9th, 2013
	B. minor	Buyenzi Market, Bujumbura, Burundi	September 4th, 2013
	Hemibates stenosoma (Boulenger, 1901)	Buyenzi Market, Bujumbura, Burundi	September 25th, 2013

Other host: Bathybates fasciatus Boulenger, 1901; *B. vittatus* Boulenger, 1914
Infection site: gill filaments
Type locality: Mpala (Lake Tanganyika, D.R.Congo) (6°44′53″S, 29°31′59″E), purchase from fishermen, April 21st, 2010, on type host and *B. vittatus* (MRAC B0-12-P-525)
Other locality: Kilomoni Market (3°20′S, 29°09′E) (Uvira, D.R.Congo), purchase from market, March 2013, on type host and *B. fasciatus*
Material studied: 20 individuals (12 from *B. minor*, five from *B. fasciatus*, three from *B. vittatus*)
Type material: holotype: MRAC 37738; paratypes: MRAC 37739, MNHN HEL415
Etymology: the specific epithet refers to the cassowaries, birds belonging to *Casuarius* Brisson, 1760 (Struthioniformes, Casuariidae), as the distal end of the accessory piece of the MA of the species is reminiscent of the crest on the head of these birds.
Description: relatively large worms with adults 915 (766–1105, $n = 19$) long, 180 (116–262, $n = 19$) wide at mid-body. Pharynx is 51 (40–72, $n = 20$) at widest. Firm anchors with clearly separated blade. Dorsal anchors with arched blade and pronounced asymmetry between guard and shaft, as guard is three times longer than shaft: $a = 58 \pm 2.8$ (52–64, $n = 32$), $b = 40 \pm 2$ (35–44, $n = 32$), $c = 8 \pm 1.3$ (6–11, $n = 32$), $d = 24 \pm 1.9$ (20–27, $n = 32$), $e = 15 \pm 0.8$ (13–17, $n = 32$). Dorsal transverse bar simple, large, thick with weakly developed auricles: $x = 71$ (64–85, $n = 20$), $y = 30$ (23–40, $n = 20$), $w = 15$ (12–20, $n = 19$), $h = 17 \pm 1.8$ (13–23, $n = 40$). Ventral anchor large, with guard two times longer than shaft: $a = 51 \pm 2.5$ (47–59, $n = 35$), $b = 43 \pm 1.7$ (39–47, $n = 35$), $c = 8 \pm 1.5$ (5–11, $n = 35$), $d = 17 \pm 1.6$ (12–19, $n = 35$), $e = 16 \pm 1.5$ (12–20, $n = 35$). Ventral transverse bar simple, V-shaped, thick, in two distinct parts (visible central connection): $x = 59 \pm 3.2$ (54–67, $n = 39$), $w = 9$ (7–12, $n = 20$). Uncinuli I long (but not thick) (sensu Pariselle & Euzet, 2003, 2009: proportional to the second pair of uncinuli) $= 30 \pm 1.2$ (27–33, $n = 30$) long; II (of larval size) $= 11$ (10–12, $n = 17$) long; III to VII of medium size (sensu Pariselle & Euzet, 2003, 2009) $= 23 \pm 1.9$ (19–28, $n = 120$) long. Penis, beginning in an ovoid bulb, straight and pointed, with distal external wall exhibiting a typical spirally coiled thickening: Pe $= 37$ (34–44, $n = 20$). Heel of the MA extremely long and slender; blunt distal end, often with constriction near to it: He $= 47$ (40–59, $n = 20$). Simple and thin accessory piece often extending beyond penis and ending in a well-developed enlarged and bulbous extremity, attached by a filament to the distal extremity of the basal bulb: Ap $= 31$ (26–38, $n = 20$). Large tubular vagina, with proximal half surrounded by a thin sheath $L = 46$ (36–59), $l = 7$ (5–8).
Remarks: In view of the spirally coiled thickening in the wall of the penis (copulatory tube), *Cichlidogyrus casuarinus* sp. nov. is reminiscent of its only two congeners for which such a feature is known: *C. centesimus* Vanhove, Volckaert & Pariselle, 2011 and *C. nshomboi* Muterezi Bukinga, Vanhove, Van Steenberge & Pariselle, 2012. An overview of the genital morphology of the three species is depicted in Fig. 4. It should be noted that these two species, like *C. casuarinus* sp. nov., possess a sclerotised vagina (not mentioned in their original descriptions) (Fig. 4d–f). The new species can be easily distinguished from *C. centesimus* by the possession of an accessory piece in the MA (*versus* absent in *C. centesimus*). On the other hand, *C. nshomboi* has an accessory piece; however, its end is less well-developed than in *C. casuarinus* sp. nov. In *C. nshomboi*, the accessory piece is somewhat thickened at the end along its main axis, whereas in *C. casuarinus* sp. nov. this thickening represents a larger portion of the length of the accessory piece, the distal end of which is often kinked. Moreover, *C. casuarinus* sp. nov. displays a longer penis (37 vs. 25) and an even longer heel than *C. nshomboi*. While in *C. nshomboi* the heel is almost as long as the penis, it is longer than the penis in *C. casuarinus* sp. nov.

Similar *Cichlidogyrus* specimens (Fig. 5) were found on other hosts and localities (Table 1). Voucher specimens are deposited in the invertebrate collection of the RMCA under MRAC 37758-37767. They differ from *C. casuarinus* sp. nov. in having an even longer heel and more stout anchor shafts and guards, that display less asymmetry. Awaiting more extensive geographic and taxon coverage and genetic confirmation, we cannot ascertain at present whether these flatworms belong to *C. casuarinus* sp. nov. or whether these morphological differences are more than intraspecific variation (see below). They hence do not form part of the type series and are referred to as *C.* cf. *casuarinus* sp. nov. A preliminary survey of *Bathybates graueri* Steindachner, 1911 hitherto did not yield any *Cichlidogyrus* parasites (*nobis*; N. Kmentová, pers. comm.).

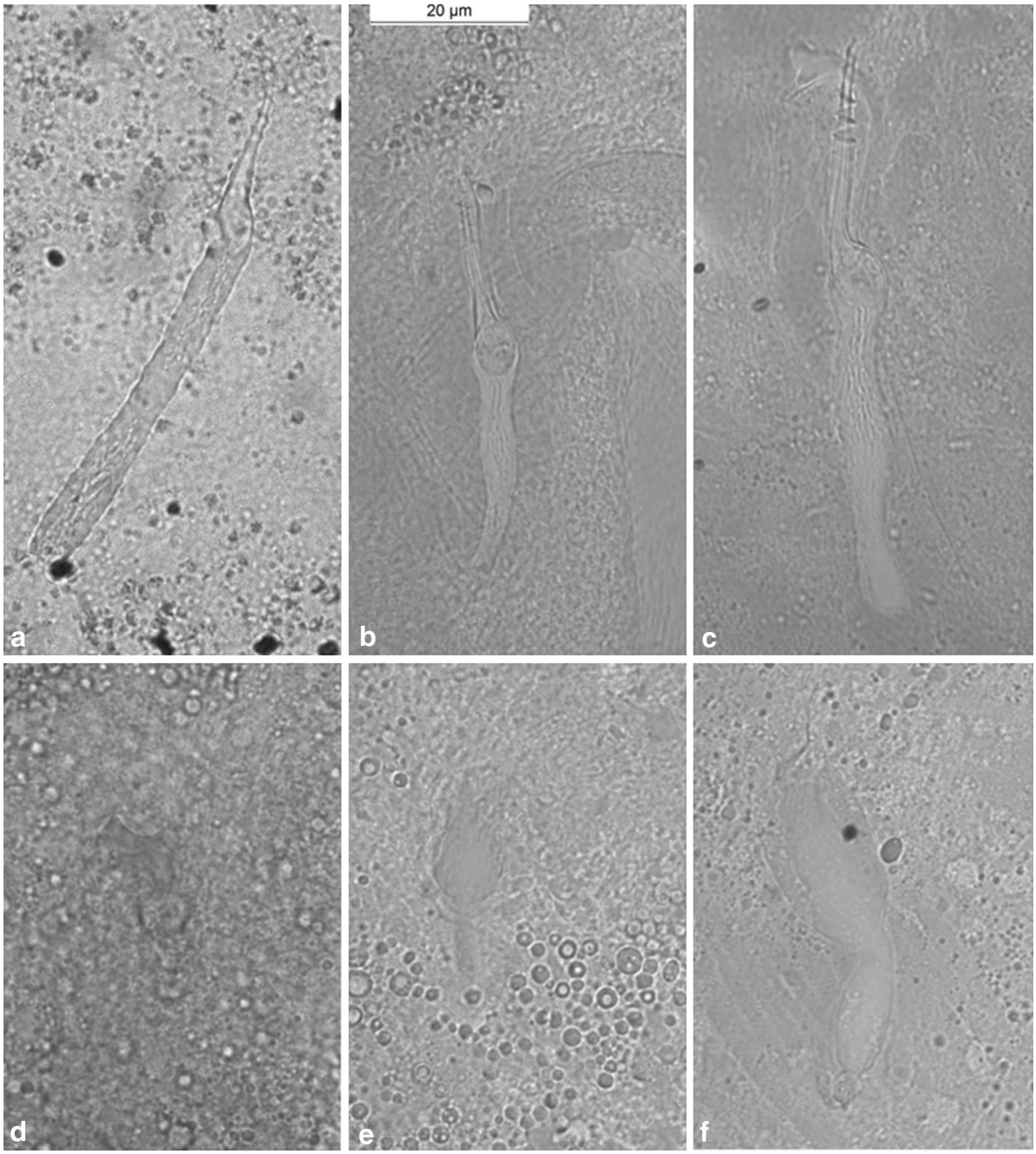
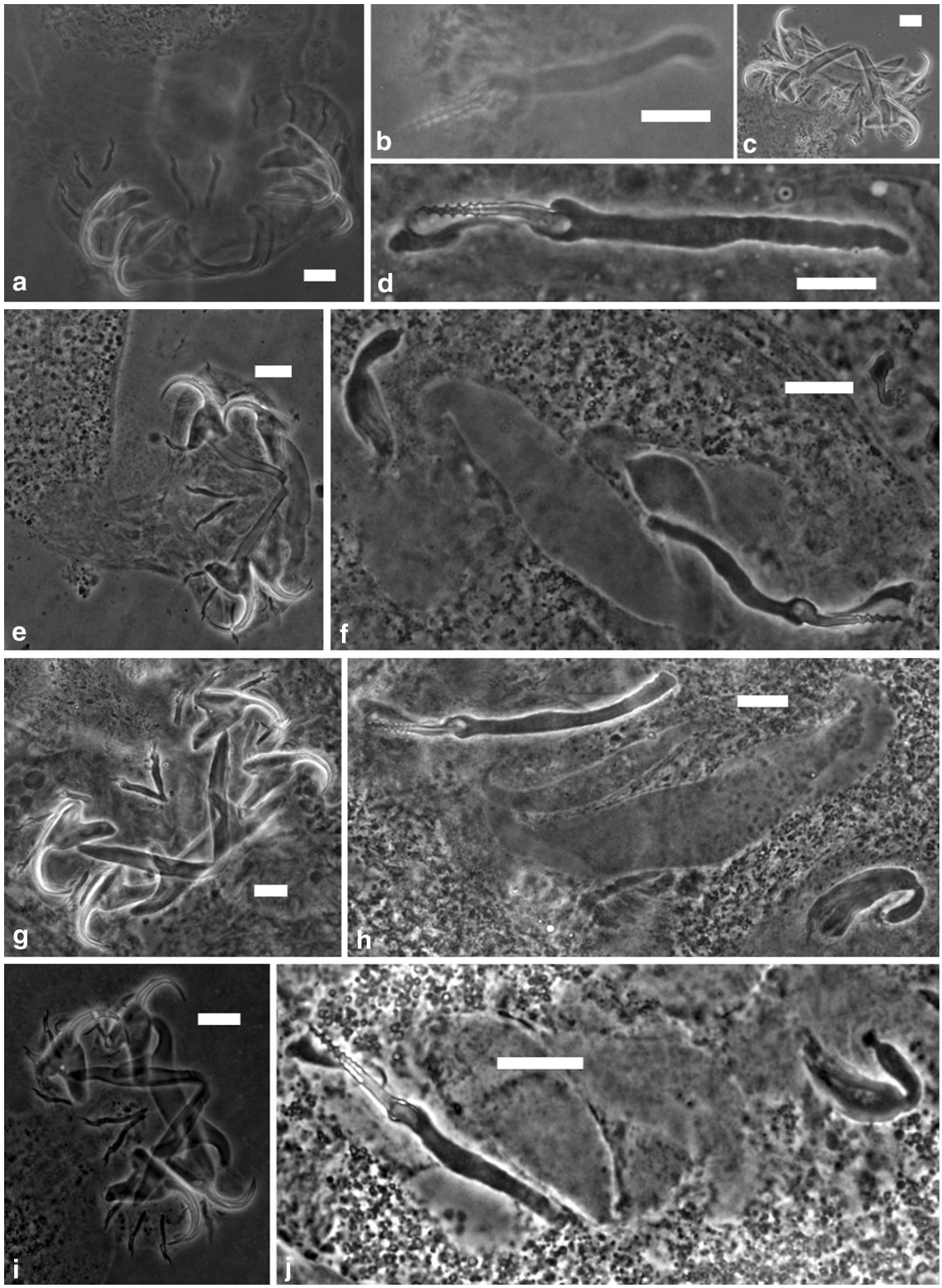


Fig. 4 Comparison of genital morphology of the three *Cichlidogyrus* species known to display a spirally-coiled thickening of the penis wall. **a** Male apparatus of *C. centesimus*, **b** male apparatus of *C. nshomboi*, **c** male apparatus of *C. casuarinus* sp. nov., **d** vagina of *C. centesimus*, **e** vagina of *C. nshomboi*, **f** vagina of *C. casuarinus* sp. nov. All micrographs displayed to scale

Discussion

The enormous diversity of Lake Tanganyika, with its species flocks of fish and its importance as cradle and reservoir of ancient fish lineages that seeded other radiations, has resulted in a significant body of literature in the fields of biodiversity and evolution (Salzburger et al., 2002, 2005; Koblmüller et al.,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◀ **Fig. 5** Micrographs of the hard parts of representatives of *Cichlidogyrus* cf. *casuarinus* sp. nov. **a** Haptor, parasite of *Bathybates leo* from Uvira (D.R.Congo), **b** male apparatus, parasite of *B. leo* from Uvira, **c** haptor, parasite of *B. fasciatus* from Uvira, **d** male apparatus, parasite of *B. fasciatus* from Uvira, **e** haptor, parasite of *B. minor* from Bujumbura (Burundi), **f** vagina and male apparatus, parasite of *B. minor* from Bujumbura, **g** haptor, parasite of *B. fasciatus* from Bujumbura, **h** male apparatus and vagina, parasite of *B. fasciatus* from Bujumbura, **i** haptor, parasite of *Hemibates stenosoma* from Bujumbura, **j** male apparatus and vagina, parasite of *H. stenosoma* from Bujumbura. Specimens fixed in Hoyer's medium and pictured under phase contrast with an Olympus BX61 microscope and Olympus Stream Motion v.1.5.1 software. *Scale bars* 20 µm

2008). The lake also contains several invertebrate taxa that underwent radiation in situ (Fryer, 1991, 2006). The parasite fauna of Lake Tanganyika fishes has come under renewed scrutiny, and 15 monogenean flatworms have lately been described from cichlids (Vanhove et al., 2011a, b; Gillardin et al., 2012; Muterezi Bukinga et al., 2012). Twelve of these belong to the most species-rich monogenean genus infecting cichlid hosts, *Cichlidogyrus* (see Pariselle & Euzet, 2009). It should be noted that the first (ancyrocephalid) monogenean species to be described from Lake Tanganyika seems to have been *Ancyrocephalus limnotrissae* Paperna, 1973 from the clupeid *Limnothrissa miodon* (Boulenger, 1906b), contrary to what was suggested by Vanhove et al. (2011a, b).

No monogeneans had hitherto been reported from the Lake's deepwater cichlid fauna. After investigation of a number of bathybatine cichlids, non-littoral piscivores, we describe a single parasite species, *Cichlidogyrus casuarinus* sp. nov. It infects *Bathybates fasciatus*, *B. minor* and *B. vittatus*. In our limited sampling, no bathybatine was found to host more than one *Cichlidogyrus* species. This may corroborate the suggestion by Vanhove (2012) that good dispersers without strong genetic population structure, as is the case for Bathybatini (see above), host relatively species-poor *Cichlidogyrus* communities. Moreover, *Cichlidogyrus* representatives recovered from *Bathybates leo* and *Hemibates stenosoma* may be conspecific, and are at the very least remarkably similar. They do exhibit some morphological variability, which is, for instance, easily noticed in the length of the MA heel. However, this does not necessarily warrant the delineation of additional species. Indeed, in the very similar *Cichlidogyrus centesimus*, this character displays substantial variation (Vanhove et al., 2011b). Moreover, generalist monogenean species are known to exhibit more haptoral morphological variation than specialists (e.g. Kaci-Chaouch et al., 2008 for *Lamellodiscus* Johnston & Tiegs, 1922 parasites of sparids; Šimková et al., 2013 for *Thaparocleidus* Jain, 1952 infecting pangasiid catfishes); hence the differences in anchor morphology may represent intraspecific variation. More intensive sampling and genetic characterisation are recommended to delineate differences within and between species. In any case, the *Cichlidogyrus* fauna of Bathybatini seems species-poor, and its representatives infect a range of host species.

There are various mechanisms through which a parasite can exploit a relatively wide host range, for example when the host trait needed by the parasite is a widespread plesiomorphy. In that sense, host range is often not a very straightforward measure of host or resource specialisation in a parasite species (e.g. Brooks et al., 2006; Agosta et al., 2010). In view of the mostly scattered studies on Lake Tanganyika parasites (see Introduction), it is too early for general conclusions on host-specificity in this system. However, some trends may appear from Table 2, comparing the host range and endemicity of dactylogyridean gill parasites of the African Great Lakes, all belonging to *Cichlidogyrus* or to *Scutogyrus* Pariselle & Euzet 1995b, a genus phylogenetically placed within *Cichlidogyrus* (Mendlová et al., 2010). It should be noted, however, that this is only the tip of the iceberg—for example, none of these parasites has been identified to species level for Lake Malawi cichlids (Table 2). Outside of Lake Tanganyika, there are species infecting several host cichlid species that are not closely related. This is the case not only in Lake Victoria (Table 2) but also in e.g. West Africa (Mendlová et al., 2012) and the Bangweulu Wetlands (Vanhove et al., 2013). Many of the Lake Tanganyika gill monogeneans, or even morphotypes, seem endemic to the Lake and more specialized towards their hosts (Table 2). This may be a consequence of currently limited sampling. However, this apparent endemicity for Lake Tanganyika may be related to the physicochemical differences with adjacent water bodies (see e.g. Coulter, 1991). In turn, the older age of Lake Tanganyika cichlids compared to the Victoria and Malawi flocks (Danley et al., 2012) may have given the parasites sufficient time for isolation and

Table 2 Overview of all species belonging to *Cichlidogyrus* and *Scutogyrus* and reported from the African Great Lakes: Lake Malawi, Lake Tanganyika and Lake Victoria

Lake	Cichlid tribe	General remarks	Parasite species	Type host	Additional African Great Lake host(s)	Specific remarks
Lake Malawi	Haplochromini	No species-level parasite identification available	*Cichlidogyrus* sp.		*Maylandia emmiltos* (Stauffer, Bowers, Kellogg & McKaye, 1997)	
					Maylandia fainzilberi (Staeck, 1976)	
Lake Tanganyika	Bathybatini	Endemicity and low host-specificity; typical Tanganyika morphotype (of male genitalia)	*Cichlidogyrus casuarinus* sp. nov., *C.* cf. *casuarinus* sp. nov.	*Bathybates minor* 1906b	*Bathybates fasciatus* Boulenger, 1901	Male apparatus with spirally-coiled thickening of the penis wall, unique for Cichlidogyrus to Lake Tanganyika
					Bathybates vittatus Boulenger, 1914	
					Bathybates leo Poll, 1956	
					Hemibates stenosoma (Boulenger, 1901)	
	Boulengerochromini	Endemicity and host-specificity; typical Tanganyika morphotype (of male genitalia)	*C. nshomboi* Muterezi Bukinga, Vanhove, Van Steenberge & Pariselle, 2012	*Boulengerochromis microlepis* (Boulenger, 1899)		Male apparatus with spirally-coiled thickening of the penis wall
	Ectodini	Endemicity and relatively high host-specificity; combination of unique Tanganyika morphotypes (of male genitalia and haptor) and haptoral morphotype known outside of Lake Tanganyika	*C. centesimus* Vanhove, Volckaert & Pariselle, 2011	*Ophthalmotilapia ventralis* (Boulenger, 1898)	*Ophthalmotilapia boops* (Boulenger, 1901)	Male apparatus with spirally-coiled thickening of the penis wall; also unique configuration of haptoral uncinuli

Table 2 continued

Lake	Cichlid tribe	General remarks	Parasite species	Type host	Additional African Great Lake host(s)	Specific remarks
					Ophthalmotilapia nasuta (Poll & Matthes 1962)	
			C. makasai Vanhove, Volckaert & Pariselle, 2011	*Ophthalmotilapia ventralis* (Boulenger, 1898)	*Ophthalmotilapia boops* (Boulenger, 1901)	Haptor with very long dorsal bar auricles, unique for *Cichlidogyrus* to Lake Tanganyika
					Ophthalmotilapia nasuta (Poll & Matthes 1962)	
			C. vandekerkhovei Vanhove, Volckaert & Pariselle, 2011	*Ophthalmotilapia ventralis* (Boulenger, 1898)	*Ophthalmotilapia boops* (Boulenger, 1901)	Haptor with extremely long dorsal bar auricles, unique for *Cichlidogyrus* to Lake Tanganyika
					Ophthalmotilapia nasuta (Poll & Matthes, 1962)	
			C. sturmbaueri Vanhove, Volckaert & Pariselle, 2011	*Ophthalmotilapia ventralis* (Boulenger, 1898)	*Ophthalmotilapia nasuta* (Poll & Matthes 1962)	Common haptoral configuration
	Haplochromini	Endemicity and host-specificity; haptoral and genital morphotype known from cichlids within and outside of Lake Tanganyika	*C. gillardinae* Muterezi Bukinga, Vanhove, Van Steenberge & Pariselle, 2012	*Astatotilapia burtoni* (Günther, 1984)		*C. gillardinae* resembles congeners reported from haplochromine, "tilapiine" and tropheine cichlids
	"tilapiines"	Combination of an endemic and host-specific species and species shared with other cichlids	*C. mbirizei* Muterezi Bukinga, Vanhove, Van Steenberge & Pariselle, 2012	*Oreochromis tanganicae* (Günther, 1894)		*C. mbirizei* is only known from Lake Tanganyika
			C. halli (Price & Kirk, 1967)	*Oreochromis shiranus* Boulenger, 1897 (from Upper Shire River, Malawi)	*Oreochromis tanganicae* (Günther, 1894)	See below

Table 2 continued

Lake	Cichlid tribe	General remarks	Parasite species	Type host	Additional African Great Lake host(s)	Specific remarks
			Scutogyrus gravivaginus (Paperna & Thurston, 1969)	*Oreochromis leucostictus* (Trewavas, 1933)	*Oreochromis tanganicae* (Günther, 1894)	See below
	Tropheini	Endemicity and relatively high host-specificity, also in non-described species	*C. gistelincki* Gillardin, Vanhove, Pariselle, Huyse & Volckaert, 2012	"*Ctenochromis*" *horei* (Günther, 1894)		*C. gistelincki* resembles congeners reported from haplochromine, "tilapiine" and tropheine cichlids
			C. irenae Gillardin, Vanhove, Pariselle, Huyse & Volckaert, 2012	"*Gnathochromis*" *pfefferi* (Boulenger, 1898)		*C. irenae* resembles congeners reported from haplochromine, "tilapiine" and tropheine cichlids
			C. steenbergei Gillardin, Vanhove, Pariselle, Huyse & Volckaert, 2012	*Limnotilapia dardennii* (Boulenger, 1899)		*C. steenbergei* resembles congeners reported from haplochromine, "tilapiine" and tropheine cichlids
	Tylochromini	Endemicity and host-specificity; haptoral morphotype typical for tylochromines elsewhere in Africa	*C. mulimbwai* Muterezi Bukinga, Vanhove, Van Steenberge & Pariselle, 2012	*Tylochromis polylepis* (Boulenger, 1900)		
			C. muzumanii Muterezi Bukinga, Vanhove, Van Steenberge & Pariselle, 2012	*Tylochromis polylepis*		
			C. sp. "*T. polylepis* 3"	*Tylochromis polylepis*		
Lake Victoria	Haplochromini	Low endemicity and low host-specificity; species often shared with other cichlid tribes	*C. bifurcatus* Paperna, 1960	*Haplochromis flaviijosephi* (Lortet, 1883) (from Israel)	*Haplochromis* sp.	Reported from *Oreochromis aureus* (Steindachner, 1864) in Israel and numerous *Haplochromis* Hilgendorf, 1988 species in Lakes Albert, George and surrounds

Table 2 continued

Lake	Cichlid tribe	General remarks	Parasite species	Type host	Additional African Great Lake host(s)	Specific remarks
			C. dionchus Paperna, 1968	*Sarotherodon galilaeus* (Linnaeus, 1758) (from Ghana)	*Haplochromis guiarti* (Pellegrin, 1904b)	Described from Lake Victoria as *C. brevicirrus* Paperna & Thurston, 1969, a junior synonym of *C. dionchus*; *C. dionchus* is also found on *Chromidotilapia guentheri* (Sauvage, 1882) in Ghana (its alleged occurrence on *Hemichromis fasciatus* Peters, 1857 actually refers to *Cichlidogyrus falcifer* Dossou & Birgi, 1984)
					Haplochromis longirostris (Hilgendorf, 1888)	
					Haplochromis obesus (Boulenger, 1906a)	
					Haplochromis obliquidens (Hilgendorf, 1888)	
					Haplochromis retrodens (Hilgendorf, 1888)	
					Haplochromis sp.	
					Tilapia zillii (Gervais, 1848)	

Table 2 continued

Lake	Cichlid tribe	General remarks	Parasite species	Type host	Additional African Great Lake host(s)	Specific remarks
			C. haplochromii Paperna & Thurston, 1969	*Haplochromis guiarti* (Pellegrin, 1904b)	*Haplochromis longirostris* (Hilgendorf, 1888)	*C. haplochromii* also infects *Haplochromis* species in Lakes Albert, George and surrounds, and *Pharyngochromis acuticeps* (Steindachner, 1866) in Lake Kariba. The hosts mentioned here include the *Haplochromis* hosts reported from *C. tubicirrus* Paperna, 1979, following Pariselle & Euzet (2009). The alleged occurrence of *C. tubicirrus* on *Oreochromis leucostictus* (Trewavas, 1933) most likely refers to *C. tilapiae* specimens (see below).
					Haplochromis macrognathus Regan, 1922	
					Haplochromis nubilus (Boulenger, 1906a)	
					Haplochromis obesus (Boulenger, 1906a)	
					Haplochromis obliquidens	
					Haplochromis retrodens	
					Haplochromis sp.	
					Macropleurodus bicolor (Boulenger, 1906a)	

Table 2 continued

Lake	Cichlid tribe	General remarks	Parasite species	Type host	Additional African Great Lake host(s)	Specific remarks
					Platytaeniodus degeni Boulenger, 1906a	
					Tilapia sp.	
			C. longipenis Paperna & Thurston, 1969	*Astatoreochromis alluaudi* Pellegrin, 1904a		
	"tilapiines"	Low endemicity and low host-specificity; species often shared with other cichlid tribes	*C. cirratus* Paperna, 1964	*Sarotherodon galilaeus* (Linnaeus, 1758) (from Israel)	*Oreochromis esculentus* (Graham, 1928)	Reported from Lake Victoria as *C. nematocirrus* Paperna, 1969, a junior synonym of *C. cirratus*; *C. cirratus* is also known from *O. niloticus* (Linnaeus, 1758) from Ghana and Lake Albert, and on *T. zillii* from Lake Albert
					Oreochromis variabilis	
			C. sclerosus Paperna & Thurston, 1969	*Oreochromis mossambicus* (Peters, 1852) (from Kajansi Ponds, Uganda)	*Oreochromis leucostictus*	*C. sclerosus* is known from a range of cichlid hosts in East and southern Africa, as well as from captivity in other parts of the world
			C. halli Paperna, 1979	*Oreochromis variabilis* (Boulenger, 1906a)	*Oreochromis esculentus*	*C. halli* infects a wide range of cichlid hosts throughout West, East and southern Africa
			C. thurstonae Ergens, 1981	*Oreochromis niloticus* (from Egypt)	*Haplochromis longirostris*	Originally reported from Lake Victoria as *C. tiberianus*; *C. thurstonae* infects a range of cichlid hosts in West and East Africa and in captivity elsewhere
					Oreochromis esculentus	

Table 2 continued

Lake	Cichlid tribe	General remarks	Parasite species	Type host	Additional African Great Lake host(s)	Specific remarks
					Oreochromis variabilis	
			C. tiberianus Paperna, 1960	*Tilapia zillii*		*C. tiberianus* infects a wide range of cichlids throughout North, West, East and southern Africa and the Middle East
			C. tilapiae Paperna, 1960	*Sarotherodon galilaeus* (from Israel)	*Haplochromis macrognathus*	*C. tilapiae* infects a wide range of cichlids throughout North, West, East and southern Africa, Israel and in captivity elsewhere in the world
					Oreochromis leucostictus	
					Oreochromis variabilis	
			Scutogyrus gravivaginus	*Oreochromis leucostictus*	*Oreochromis variabilis*	*S. gravivaginus* is also known from *Oreochromis mortimeri* (Trewavas, 1966) from Lake Kariba

Parasite species are arranged per lake and per host cichlid tribe; type host and additional hosts are provided, as well as remarks on endemicity and host range, per host tribe and per parasite species. Parasite species were originally described from the respective lakes unless otherwise mentioned under the type host. Only hosts retrieved from the African Great Lakes proper are taken into account. For example, the monogeneans reported by Muterezi Bukinga et al. (2012) from *Oreochromis niloticus* from wetlands adjacent to Lake Tanganyika, are not considered Lake Tanganyika monogeneans. Based on Paperna (1979), Douëllou (1993), Blais et al. (2007), Pariselle & Euzet (2009), Vanhove et al. (2011b), Vanhove (2012), Gillardin et al. (2012), Muterezi Bukinga et al. (2012) and the current study

specialization. In any case, the host range of *Cichlidogyrus casuarinus* sp. nov. is in stark contrast with the narrow host-specificity reported for littoral Tanganyika cichlids by Vanhove (2012). Nevertheless, Vanhove et al. (2011b) reported several members of *Ophthalmotilapia* Pellegrin 1904a, that do not form a monophyletic group (Koblmüller et al., 2004), to share *Cichlidogyrus* species. However, these species have undergone introgressive hybridization (Nevado et al., 2011). According to Moulia (1999), host hybridization may indeed increase host range. Given the importance of hybridization in various Lake Tanganyika cichlid tribes (Rüber et al., 2001; Nevado et al., 2009; Koblmüller et al., 2010), one could expect this to have an influence on the host range of many Tanganyika cichlid parasites. However, Kirchberger et al. (2012) did not find evidence for hybridization in bathybatines. *Cichlidogyrus casuarinus* sp. nov. seems to parasitize hosts that have stayed reproductively isolated since early in their evolutionary history.

Considering the position of its hosts *Bathybates fasciatus*, *B. minor* and *B. vittatus* in the Bathybatini phylogeny, *Cichlidogyrus casuarinus* sp. nov. infects bathybatines across a large span of their phylogenetic range. These hosts even differ clearly from each other in feeding ecology and spatial distribution (Kirchberger et al., 2012). We hypothesize that this host range is an adaption to lower host availability in non-littoral waters. This observation was also made in monogeneans of marine deepwater fishes (Justine et al., 2012; Schoelinck et al., 2012). Indeed, *C. casuarinus* sp. nov. is expected to have evolved some adjustments in its life cycle and infection strategy. Normally, dactylogyrid eggs develop and hatch on the water bottom, after which a free-living oncomiracidium larva encounters a host (Paperna, 1996). This strategy seems difficult when targeting pelagic and/or deepwater fishes like bathybatines, or at least would not allow for high host-specificity in view of low host availability.

Obviously, improved sample size and other sampling seasons would be needed to estimate more reliably the true diversity of the parasite community of bathybatines. Detailed morphometric and genetic work is ongoing to check for host adaptation and cryptic or incipient speciation (Kmentová et al., unpubl.). Indeed, sequence analysis has suggested cryptic *Cichlidogyrus* species infecting "tilapiines" to be more host-specific than presumed for their "overarching" species (Pouyaud et al., 2006). Moreover, ongoing speciation as a result of adaptation to sympatric host species has been observed in monogeneans as well (Bueno-Silva et al., 2011 for gyrodactylid parasites of callichthyid catfishes). Whether or not such phenomenon is acting on *C. casuarinus* sp. nov. as well, this monogenean (lineage) has a host range including phylogenetically, trophically and spatially quite different fishes. This strongly suggests a different host range within *Cichlidogyrus* when infecting host lineages that differ ecologically. Host ecology emerges in several studies as an important factor determining host range and disease transmission (Cobey et al., 2010; Cooper et al., 2012). Lake Tanganyika, and the African Great Lakes in general, offer us a diverse assemblage of closely related and much less related cichlids exploiting a wide range of ecological niches. Representatives from the same parasite, the monogenean species belonging to *Cichlidogyrus* with their simple life cycle, have been observed from a selection of ecologically different cichlid host species. We are convinced that Great Lake *Cichlidogyrus* has high potential as a model for the influence of host ecology on disease evolution, and as a model to understand how phylogenetic and ecological aspects together mediate a parasite's host-switching potential.

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References

Agosta, S. J., N. Janz & D. R. Brooks, 2010. How specialists can be generalists: resolving the "parasite paradox" and implications for emerging infectious disease. Zoologia (Curitiba) 27: 151–162.

Blais, J., C. Rico, C. van Oosterhout, J. Cable, G. F. Turner & L. Bernatchez, 2007. MHC adaptive divergence between closely related and sympatric African cichlids. PLoS One 2(8): e734.

Boulenger, G. A., 1897. Descriptions of new fishes from the Upper Shiré River, British Central Africa, collected by Dr. Percy Rendall, and presented to the British Museum by Sir Harry H. Johnston, K. C. B. Proceedings of the Zoological Society of London 1896(part 4): 915–920.

Boulenger, G. A., 1898. Report on the fishes recently obtained by Mr. J. E. S. Moore in Lake Tanganyika. Proceedings of the Zoological Society of London 1898(part 3): 494–497.

Boulenger, G. A., 1899. Second contribution to the ichthyology of Lake Tanganyika. On the fishes obtained by the Congo Free State Expedition under Lieut. Lemaire in 1898. Transactions of the Zoological Society of London 15(part 4) (1): 87–96.

Boulenger, G. A., 1900. Matériaux pour la faune du Congo. Poissons nouveaux du Congo. Sixième Partie. Mormyres, Characins, Cyprins, Silures, Acanthoptérygiens, Dipneustes. Annales du Musee du Congo (Sér. Zoologie) 1(fasc. 6): 129–164.

Boulenger, G. A., 1901. Diagnoses of new fishes discovered by Mr. J. E. S. Moore in lakes Tanganyika and Kivu. II. Cichlidae, Mastacembelidae. Annals and Magazine of Natural History (Series 7) 7: 1–6.

Boulenger, G. A., 1906a. Descriptions of new fishes discovered by Mr. E. Degen in Lake Victoria. Annals and Magazine of Natural History (Series 7) 17(101): 433–452.

Boulenger, G. A., 1906b. Fourth contribution to the ichthyology of Lake Tanganyika. Report on the collection of fishes made by Dr. W. A. Cunnington during the Third Tanganyika Expedition, 1904–1905. Transactions of the Zoological Society of London 17: 537–601.

Boulenger, G. A., 1914. Mission Stappers au Tanganyika-Moero. Diagnoses de poissons nouveaux. I. Acanthoptérygiens, Opisthomes, Cyprinodontes. Revue Zoologique Africaine 3: 442–447.

Brooks, D. R., 1993. Extending the symbiotype concept to host voucher specimens. Journal of Parasitology 79(4): 631–633.

Brooks, D. R., V. León-Règagnon, D. A. McLennan & D. Zelmer, 2006. Ecological fitting as a determinant of the community structure of platyhelminth parasites of anurans. Ecology 87: S76–S85.

Bueno-Silva, M., W. A. Boeger & M. R. Pie, 2011. Choice matters: incipient speciation in *Gyrodactylus corydori* (Monogenoidea: Gyrodactylidae). International Journal for Parasitology 41: 657–667.

Choudhury, A. & T. A. Dick, 2000. Richness and diversity of helminth communities in tropical freshwater fishes: empirical evidence. Journal of Biogeography 27: 935–956.

Cobey, S., M. Pascual & U. Dieckmann, 2010. Ecological factors driving the long-term evolution of influenza's host range. Proceedings of the Royal Society of London B: Biological Sciences 277: 2803–2810.

Cooper, N., R. Griffin, M. Franz, M. Omotayo & C. L. Nunn, 2012. Phylogenetic host specificity and understanding parasite sharing in primates. Ecology Letters 15: 1370–1377.

Coulter, G. W., 1991. Composition of the flora and fauna. In Coulter, G. W. (ed.), Lake Tanganyika and its Life. Oxford University Press, Oxford: 200–274.

Danley, P. D., M. Husemann, B. Ding, L. M. DiPietro, E. J. Beverly & D. J. Peppe, 2012. The impact of the geologic history and paleoclimate on the diversification of East African cichlids. International Journal of Evolutionary Biology 2012: 574851.

de Beauchamp, P. M., 1914. Sur quelques parasites provenant du Congo belge. Revue de Zoologie et de Botanique Africaines 4: 109–116.

Dossou, C. & E. Birgi, 1984. Monogènes parasites d'*Hemichromis fasciatus* Peters, 1857 (Teleostei, Cichlidae). Annales des Sciences Naturelles, Zoologie 6: 101–109.

Douëllou, L., 1993. Monogeneans of the genus *Cichlidogyrus* Paperna, 1960 (Dactylogyridae: Ancyrocephalinae) from cichlid fishes of Lake Kariba (Zimbabwe) with descriptions of five new species. Systematic Parasitology 25: 159–186.

Ergens, R., 1981. Nine species of the genus *Cichlidogyrus* Paperna, 1960 (Monogenea: Ancyrocephalinae) from Egyptian fishes. Folia Parasitologica 28: 205–214.

Eschmeyer, W. N. (ed), 2013. Catalog of fishes: genera, species, references [available on internet at http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp]. Accessed 14 December 2013.

Euzet, L. & M. Prost, 1981. Report of the meeting on Monogenea: problems of systematics, biology and ecology. In Slusarski, W. (ed.), Review of Advances in Parasitology. P.W.N. Polish Scientific Publishers, Warsaw: 1003–1004.

Fain, A., 1961. Les Pentastomides de l'Afrique Centrale. Annalen Koninklijk Museum voor Midden-Afrika Serie in-8°. Zoologische Wetenschappen 92: 1–115.

Frey, J. K., T. L. Yates, D. W. Duszynski, W. L. Gannon & S. L. Gardner, 1992. Designation and curatorial management of type host specimens (symbiotypes) for new parasite species. Journal of Parasitology 78(5): 930–932.

Fryer, G., 1968. The parasitic Crustacea of African freshwater fishes: their biology and distribution. Journal of Zoology 156: 45–95.

Fryer, G., 1991. Comparative aspects of adaptive radiation and speciation in Lake Baikal and the great rift lakes of Africa. Hydrobiologia 211: 137–146.

Fryer, G., 2006. Evolution in ancient lakes: radiation of Tanganyikan atyid prawns and speciation of pelagic cichlid fishes in Lake Malawi (Coulter, G., O. Timoshkin, L. Timoshkina & K. Martens (eds) Species and speciation in ancient lakes). Hydrobiologia 568: 131–142.

Fuhrmann, O. & J. G. Baer, 1925. Report on the Cestoda. Zoological results of the Third Tanganyika Expedition (1904–1905). Proceedings of the Zoological Society of London 1(6–7): 79–100.

Gervais, F. L. P., 1848. Sur les animaux vertébrés de l'Algérie, envisagés sous le double rapport de la géographie zoologique et de la domestication. Annales des Sciences Naturelles, Paris (Zoologie) (Sér. 3) 10: 202–208.

Gillardin, C., M. P. M. Vanhove, A. Pariselle, T. Huyse & F. A. M. Volckaert, 2012. Ancyrocephalidae (Monogenea) of Lake Tanganyika: II: description of the first *Cichlidogyrus* spp. parasites from Tropheini fish hosts (Teleostei, Cichlidae). Parasitology Research 110: 305–313.

Günther, A., 1889. On some fishes from Kilima-Njaro District. Proceedings of the Zoological Society of London 1889: 70–72.

Günther, A., 1894. Descriptions of the reptiles and fishes collected by Mr. E. Coode-Hore on Lake Tanganyika. Proceedings of the Zoological Society of London 1893(part 4): 628–632.

Gussev, A. V., 1962 (1964). Order Dactylogyridea. In Bychovskaya-Pavlovskaya, I. E., A. V. Gussev, M. N. Dubinina, N. A. Izymova, T. S. Smirnova, I. L. Sokolovskaya, G. A. Shtein, S. S. Shul'man & V. M. Epsthein (eds), Key to the Parasites of Freshwater Fish of the USSR. Israel Program for Scientific Translations, Jerusalem: 204–342. [Russian original: Opredelitel' parazitov presnovohnyh ryb SSSR. Izadtel'stovo Akademii Nauk SSSR, Moscow-Leningrad].

Graham, M., 1928. *Tilapia esculenta*, a new species of cichlid fish from the Victoria Nyanza, with notes on the habits of this species and the nearly-related *Tilapia variabilis*, Blgr. Annals and Magazine of Natural History (Series 10) 2(8): 209–213.

Hemmingsen, W., O. Halvorsen & K. MacKenzie, 2000. The occurrence of some metazoan parasites of Atlantic cod, *Gadus morhua* L., in relation to age and sex of the host in Balsfjord (70°N), North Norway. Polar Biology 23: 368–372.

Hett, M. L., 1924. Report on the Linguatulidae. Zoological Results of the 3rd Tanganyika Expedition (1904–1905). Proceedings of the Zoological Society of London 11: 161.

Hilgendorf, F. M., 1888. Fische aus dem Victoria-Nyanza (Ukerewe-See), gesammelt von dem verstorbenen Dr. G. A. Fischer. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1888: 75–79.

Humason, G. L., 1979. Animal Tissue Techniques, 4th ed. Freeman and Company, San Francisco.

Jain, S. L., 1952. Monogenea of Indian freshwater fishes. II. *Thaparocleidus wallagonius* n. g., n. sp. (Subfamily: Tetraonchinae) from the gills of *Wallagonia attu* (Bloch), from Lucknow. Indian Journal of Helminthology 4: 43–48.

Johnston, T. H. & O. W. Tiegs, 1922. New gyrodactyloid trematodes from Australian fishes together with a reclassification of the super-family Gyrodactyloidea. Proceedings of the Linnean Society of New South Wales 47: 83–131.

Justine, J.-L., I. Beveridge, G. A. Boxshall, R. A. Bray, F. Moravec & I. D. Whittington, 2010. An annotated list of fish parasites (Copepoda, Monogenea, Digenea, Cestoda and Nematoda) collected from emperors and emperor bream (Lethrinidae) in New Caledonia further highlights parasite biodiversity estimates on coral reef fish. Zootaxa 2691: 1–40.

Justine, J.-L., I. Beveridge, G. A. Boxshall, R. A. Bray, T. L. Miller, F. Moravec, J.-P. Trilles & I. D. Whittington, 2012. An annotated list of fish parasites (Isopoda, Copepoda, Monogenea, Digenea, Cestoda, Nematoda) collected from snappers and bream (Lutjanidae, Nemipteridae, Caesionidae) in New Caledonia confirms high parasite biodiversity on coral reef fish. Aquatic Biosystems 8: 22.

Kaci-Chaouch, T., O. Verneau & Y. Desdevises, 2008. Host specificity is linked to intraspecific variability in the genus *Lamellodiscus* (Monogenea). Parasitology 135(607–616): 2008.

Kilian, E. & A. Avenant-Oldewage, 2013. Infestation and pathological alterations by *Ergasilus sarsi* (Copepoda) on the Tanganyika Killifish from Africa. Journal of Aquatic Animal Health 25: 237–242.

Kirchberger, P. C., K. M. Sefc, C. Sturmbauer & S. Koblmüller, 2012. Evolutionary history of Lake Tanganyika's predatory deepwater cichlids. International Journal of Evolutionary Biology 2012: 716209.

Koblmüller, S., W. Salzburger & C. Sturmbauer, 2004. Evolutionary relationships in the sand-dwelling cichlid lineage of Lake Tanganyika suggest multiple colonization of rocky habitats and convergent origin of biparental mouthbrooding. Journal of Molecular Evolution 58: 79–96.

Koblmüller, S., N. Duftner, C. Katongo, H. Phiri & C. Sturmbauer, 2005. Ancient divergence in bathypelagic Lake Tanganyika deepwater cichlids: mitochondrial phylogeny of the tribe Bathybatini. Journal of Molecular Evolution 60: 297–314.

Koblmüller, S., K. M. Sefc & C. Sturmbauer, 2008. The Lake Tanganyika cichlid species assemblage: recent advances in molecular phylogenetics. Hydrobiologia 615: 5–20.

Koblmüller, S., B. Egger, C. Sturmbauer & K. M. Sefc, 2010. Rapid radiation, ancient incomplete lineage sorting and ancient hybridization in the endemic Lake Tanganyika cichlid tribe Tropheini. Molecular Phylogenetics and Evolution 55: 318–334.

Kritsky, D. C. & W. A. Boeger, 1989. The phylogenetic status of the Ancyrocephalinae Bychowsky, 1937 (Monogenea: Dactylogyroidea). Journal of Parasitology 75: 207–211.

Linnaeus, C., 1758. Systema Naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Tomus 1. Laurentii Salvii, Stockholm.

Lortet, L., 1883. Études zoologiques sur la faune du lac de Tibériade, suivies d'un aperçu sur la faune des lacs d'Antioche et de Homs. I. Poissons et reptiles du lac de Tibériade et de quelques autres parties de la Syrie. Archives du Muséum d'Histoire Naturelle de Lyon 3: 99–189.

Luque, J. L. & R. Poulin, 2008. Linking ecology with parasite diversity in Neotropical fishes. Journal of Fish Biology 72: 189–204.

Machado, M. H., G. C. Pavanelli & R. M. Takemoto, 1995. Influence of the type of environment and of the hydrological level variation in endoparasitic infrapopulations of *Pseudoplatystoma corruscans* (Agassiz) and *Schizodon borelli* (Boulenger) (Osteichthyes) of the high Paraná River, Brazil. Revista Brasileira de Zoologia 12: 961–976.

Malmberg, G., 1957. On the occurrence of *Gyrodactylus* on Swedish fishes. Skrifter utgivna av Södra Sveriges Fiskeriföreningen 1956: 19–76. [in Swedish].

Mendlová, A., A. Pariselle, M. Vyskočilová & A. Šimková, 2010. Molecular phylogeny of monogeneans parasitizing African freshwater Cichlidae inferred from LSU rDNA sequences. Parasitology Research 107: 1405–1413.

Mendlová, M., Y. Desdevises, K. Civáňová, A. Pariselle & A. Šimková, 2012. Monogeneans of West African cichlid fish: evolution and cophylogenetic interactions. PLoS One 7: e37268.

Moore, J. P., 1938. Additions to our knowledge of African leeches (Hirudinea). Proceedings of the Academy of Natural Sciences 90: 297–360.

Moulia, C., 1999. Parasitism of plant and animal hybrids: are facts and fates the same? Ecology 80: 392–406.

Muterezi Bukinga, F., M. P. M. Vanhove, M. Van Steenberge & A. Pariselle, 2012. Ancyrocephalidae (Monogenea) of Lake Tanganyika: III: *Cichlidogyrus* infecting the world's biggest cichlid and the non-endemic tribes Haplochromini, Oreochromini and Tylochromini (Teleostei, Cichlidae). Parasitology Research 111: 2049–2061.

Mwita, C. & G. Nkwengulila, 2008. Determinants of the parasite community of clariid fishes from Lake Victoria, Tanzania. Journal of Helminthology 82: 7–16.

Nevado, B., S. Koblmüller, C. Sturmbauer, J. Snoeks, J. Usano-Alemany & E. Verheyen, 2009. Complete mitochondrial DNA replacement in a Lake Tanganyika cichlid fish. Molecular Ecology 18: 4240–4255.

Nevado, B., V. Fazalova, T. Backeljau, M. Hanssens & E. Verheyen, 2011. Repeated unidirectional introgression of nuclear and mitochondrial DNA between four congeneric Tanganyikan cichlids. Molecular Biology and Evolution 28: 2253–2267.

Paperna, I., 1960. Studies on monogenetic trematodes in Israel. 2 Monogenetic trematodes of cichlids. Bamidgeh, Bulletin of Fish Culture in Israel 12: 20–33.

Paperna, I., 1964. Parasitic helminths of inland-water fishes in Israel. Israel Journal of Zoology 13: 1–26.

Paperna, I., 1968. Monogenetic trematodes collected from fresh water fish in Ghana. Second report. Bamidgeh, Bulletin of Fish Culture in Israel 20: 80–100.

Paperna, I., 1973. New species of Monogenea (Vermes) from African freshwater fish. A preliminary report. Revue de Zoologie et de Botanique Africaines 87: 505–518.

Paperna, I., 1979. Monogenea of inland water fish in Africa. Annalen Koninklijk Museum voor Midden-Afrika Serie in-8°. Zoologische Wetenschappen 226: 1–131.

Paperna, I., 1996. Parasites, infections and diseases of fishes in Africa. An update. CIFA Technical Paper 31. Food and Agriculture Organization of the United Nations, Rome.

Paperna, I. & J. P. Thurston, 1969. Monogenetic trematodes collected from cichlid fish in Uganda; including the description of five new species of *Cichlidogyrus*. Revue de Zoologie et de Botanique Africaines 79: 15–33.

Pariselle, A. & L. Euzet, 1995a. Gill parasites of the genus *Cichlidogyrus* Paperna, 1960 (Monogenea, Ancyrocephalidae) from *Tilapia guineensis* (Bleeker, 1862), with descriptions of six new species. Systematic Parasitology 30: 187–198.

Pariselle, A. & L. Euzet, 1995b. *Scutogyrus* n. g. (Monogenea, Ancyrocephalidae) for *Cichlidogyrus longicornis minus* Dossou, 1982, *C. longicornis* and *C. l. gravivaginus* Paperna and Thurston, 1969, with descriptions of three new species parasitic on African cichlids. Journal of the Helminthological Society of Washington 62: 157–173.

Pariselle, A. & L. Euzet, 2003. Four new species of *Cichlidogyrus* (Monogenea: Ancyrocephalidae), gill parasites of *Tilapia cabrae* (Teleostei: Cichlidae), with discussion on relative length of haptoral sclerites. Folia Parasitologica 50: 195–201.

Pariselle, A. & L. Euzet, 2009. Systematic revision of dactylogyridean parasites (Monogenea) from cichlid fishes in Africa, the Levant and Madagascar. Zoosystema 31: 849–898.

Pariselle, A., C. Bilong Bilong & L. Euzet, 2003a. Four new species of *Cichlidogyrus* Paperna, 1960 (Monogenea, Ancyrocephalidae), all gill parasites from African mouthbreeder tilapias of the genera *Sarotherodon* and *Oreochromis* (Pisces, Cichlidae), with a re-description of *C. thurstonae* Ergens, 1981. Systematic Parasitology 56: 201–210.

Pariselle, A., S. Morand, M. Deveney & L. Pouyaud, 2003b. Parasite species richness of closely related hosts: historical scenario and "genetic" hypothesis. In Combes, C. & J. Jourdane (eds), Hommage à Louis Euzet – taxonomie, écologie et évolution des métazoaires parasites. Taxonomy, Ecology and Evolution of Metazoan Parasites. Presses Universitaires de Perpignan, Perpignan: 147–166.

Pellegrin, J., 1904a. Contribution à l'étude anatomique, biologique et taxinomique des poissons de la famille des Cichlidés. Mémoires de la Société Zoologique de France 16: 41–400.

Pellegrin, J., 1904b. Diagnoses préliminaires de poissons nouveaux du Lac Victoria, recueillis par M. Alluaud. Bulletin de la Société Zoologique de France 29(8): 184–186.

Peters, W., 1852. Diagnosen von neuen Flussfischen aus Mossambique. Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 1852(275–276): 681–685.

Peters, W., 1857. Neue Gattung von Chromiden. Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 1857: 403.

Plaisance, L., D. T. J. Littlewood, P. D. Olson & S. Morand, 2005. Molecular phylogeny of gill monogeneans (Platyhelminthes, Monogenea, Dactylogyridae) and colonization of Indo-West Pacific butterflyfish hosts (Perciformes, Chaetodontidae). Zoologica Scripta 34: 425–436.

Poll, M., 1956. Poissons Cichlidae. Exploration Hydrobiologique du Lac Tanganika (1946–1947). Résultats Scientifiques 3: 1–619.

Poll, M., 1986. Classification des Cichlidae du lac Tanganika. Tribus, genres et espèces. Mémoires de la Classe des Sciences. Académie Royale de Belgique, Brussels.

Poll, M. & H. Matthes, 1962. Trois poissons remarquables du lac Tanganika. Annalen Koninklijk Museum voor Midden-Afrika Serie in-8°. Zoologische Wetenschappen 111: 1–26.

Poulin, R., 1995. Phylogeny, ecology, and the richness of parasite communities in vertebrates. Ecological Monographs 65: 283–302.

Pouyaud, L., E. Desmarais, M. Deveney & A. Pariselle, 2006. Phylogenetic relationships among monogenean gill parasites (Dactylogyridea, Ancyrocephalidae) infesting tilapiine hosts (Cichlidae): systematic and evolutionary implications. Molecular Phylogenetics and Evolution 38: 241–249.

Price, C. E. & R. G. Kirk, 1967. First description of a monogenetic trematode from Malawi. Revue de Zoologie et de Botanique Africaines 76: 137–144.

Prudhoe, S., 1951. Trematoda, Cestoda and Acanthocephala. Exploration Hydrobiologique du Lac Tanganyika (1946–1947). Résultats Scientifiques 3(2): 2–9.

Raeymaekers, J. A. M., P. I. Hablützel, A. F. Grégoir, J. Bamps, A. K. Roose, M. P. M. Vanhove, M. Van Steenberge, A. Pariselle, T. Huyse, J. Snoeks & F. A. M. Volckaert, 2013. Contrasting parasite communities among allopatric colour morphs of the Lake Tanganyika cichlid *Tropheus*: potential for parasite-driven speciation? BMC Evolutionary Biology 13: 41.

Regan, C. T., 1920. The classification of the fishes of the family Cichlidae. I. The Tanganyika genera. Annals and Magazine of Natural History (Series 9) 5: 33–53.

Regan, C. T., 1922. The cichlid fishes of Lake Victoria. Proceedings of the Zoological Society of London 1922 (pt 1) (9): 157–191.

Rüber, L., A. Meyer, C. Sturmbauer & E. Verheyen, 2001. Population structure in two sympatric species of the Lake Tanganyika cichlid tribe Eretmodini: evidence for introgression. Molecular Ecology 10: 1207–1225.

Salzburger, W., A. Meyer, S. Baric, E. Verheyen & C. Sturmbauer, 2002. Phylogeny of the Lake Tanganyika cichlid species flock and its relationship to the Central and East African haplochromine cichlid fish faunas. Systematic Biology 51: 113–135.

Salzburger, W., T. Mack, E. Verheyen & A. Meyer, 2005. Out of Tanganyika: genesis, explosive speciation, key-innovations and phylogeography of haplochromine cichlid fishes. BMC Evolutionary Biology 5: 17.

Sasal, P. & S. Morand, 1998. Comparative analysis: a tool for studying monogenean ecology and evolution. International Journal for Parasitology 28: 1637–1644.

Sauvage, H.-E., 1882. Notice sur les poissons du territoire d'Assinie (Côte d'Or). Bulletin de la Société Zoologique de France 7: 313–325.

Schoelinck, C., C. Cruaud & J.-L. Justine, 2012. Are all species of *Pseudorhabdosynochus* strictly host specific? A molecular study. Parasitology International 61: 356–359.

Schwarzer, J., B. Misof, D. Tautz & U. K. Schliewen, 2009. The root of the East African cichlid radiations. BMC Evolutionary Biology 9(1): 186.

Sciacchitano, I., 1962. Contributo alla conoscenza degli Irudinei dell'Africa Centrale. Revue de Zoologie et de Botanique Africaines 65(3–4): 376–381.

Šimková, A., L. Plaisance, I. Matějusová, S. Morand & O. Verneau, 2003. Phylogenetic relationships of the Dactylogyridae Bychowsky, 1933 (Monogenea: Dactylogyridea): the need for the systematic revision of the Ancyrocephalinae Bychowsky, 1937. Systematic Parasitology 54: 1–11.

Šimková, A., I. Matějusová & C. O. Cunningham, 2006. A molecular phylogeny of the Dactylogyridae sensu Kritsky & Boeger (1989) (Monogenea) based on the D1–D3 domains of large subunit rDNA. Parasitology 133: 43–54.

Šimková, A., C. Serbielle, A. Pariselle, M. P. M. Vanhove & S. Morand, 2013. Speciation in *Thaparocleidus* (Monogenea: Dactylogyridae) parasitizing Asian pangasiid catfishes. BioMed Research International 2013: 353956.

Snoeks, J., 2000. How well known is the ichthyodiversity of the large East African lakes? Advances in Ecological Research 31: 17–38.

Staeck, W., 1976. Ergebnisse einer ichthyologischen Sammelreise zum Nordende des Nyassasees (2). Aquarium Aqua Terra 10(89): 486–492.

Stauffer Jr, J. R., N. J. Bowers, K. A. Kellogg & K. R. McKaye, 1997. A revision of the blue–black *Pseudotropheus zebra* (Teleostei: Cichlidae) complex from Lake Malaŵi, Africa, with a description of a new genus and ten new species. Proceedings of the Academy of Natural Sciences of Philadelphia 148: 189–230.

Steindachner, F., 1864. Ichthyologische Mittheilungen. (VII.) Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 14: 223–232.

Steindachner, F., 1866. Ichthyologische Mittheilungen. (IX.) Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 16: 761–796.

Steindachner, F., 1911. Beiträge zur Kenntniss der Fischfauna des Tanganyikasees und des Kongogebietes. Anzeiger der Akademie der Wissenschaften in Wien 48: 528–530.

Takahashi, T., 2003. Systematics of Tanganyikan cichlid fishes (Teleostei: Perciformes). Ichthyological Research 50: 367–382.

Takemoto, R. M., G. C. Pavanelli, M. A. P. Lizama, J. L. Luque & R. Poulin, 2005. Host population density as the major determinant of endoparasite species richness in floodplain fishes of the upper Paraná River, Brazil. Journal of Helminthology 79: 75–84.

Trewavas, E., 1933. Scientific results of the Cambridge Expedition to the East African Lakes, 1930. The cichlid fishes. The Journal of the Linnean Society of London. Zoology 38(259): 309–341.

Vanhove, M. P. M., 2012. Species flocks and parasite evolution. Towards a co-phylogenetic analysis of monogenean flatworms of cichlids and gobies. PhD thesis, KU Leuven, Leuven.

Vanhove, M. P. M., J. Snoeks, F. A. M. Volckaert & T. Huyse, 2011a. First description of monogenean parasites in Lake Tanganyika: the cichlid *Simochromis diagramma* (Teleostei, Cichlidae) harbours a high diversity of *Gyrodactylus* species (Platyhelminthes, Monogenea). Parasitology 138: 364–380.

Vanhove, M. P. M., F. A. M. Volckaert & A. Pariselle, 2011b. Ancyrocephalidae (Monogenea) of Lake Tanganyika: I: four new species of *Cichlidogyrus* from *Ophthalmotilapia ventralis* (Teleostei, Cichlidae), the first record of this family in the basin. Zoologia 28: 253–263.

Vanhove, M. P. M., M. Van Steenberge, S. Dessein, F. A. M. Volckaert, J. Snoeks, T. Huyse & A. Pariselle, 2013. Biogeographical implications of Zambezian *Cichlidogyrus* species (Platyhelminthes: Monogenea: Ancyrocephalidae) parasitizing Congolian cichlids. Zootaxa 3608: 398–400.

Vanhove, M. P. M., A. N. Economou, S. Zogaris, S. Giakoumi, D. Zanella, F. A. M. Volckaert & T. Huyse, 2014. The *Gyrodactylus* (Monogenea, Gyrodactylidae) parasite fauna of freshwater sand gobies (Teleostei, Gobioidei) in their centre of endemism, with description of seven new species. Parasitology Research 113(2): 653–668. doi:10.1007/s00436-013-3693-8.

Van Steenberge, M., M. P. M. Vanhove, D. Muzumani Risasi, T. Mulimbwa N'sibula, F. Muterezi Bukinga, A. Pariselle, C. Gillardin, E. Vreven, J. A. M. Raeymaekers, T. Huyse, F. A. M. Volckaert, V. Nshombo Muderhwa & J. Snoeks, 2011. A recent inventory of the fishes of the north-western and central western coast of Lake Tanganyika (Democratic Republic Congo). Acta Ichthyologica et Piscatoria 41: 201–214.

Woodward, S. P., 1859. On some new freshwater shells from Central Africa. Proceedings of the Zoological Society of London 27: 348–350.